LIGHT EFFECTS ON TREE GROWTH AND SEED GERMINATION

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Everyone knows that trees cannot grow without light, but not *why* they require light for processes besides photosynthesis. What are some of these effects of light on trees and why are they not more widely recognized as light effects? What is the nature of the reactions in plants that make them responsive to light? These are among the questions with which we are concerned.

Photoperiodic Growth Response in Trees

Perhaps one of the most conspicuous effects of light on trees is expressed in photoperiodic control of their growth. Seedlings, rooted cuttings or young plants of many woody species continue growing or stop growing in response to long or short days, respectively. This is a conspicuous response observed and mentioned by Garner and Allard (1920) as a daylength effect, but still not widely recognized as such. Stoppage of growth is frequently attributed to low temperature, but it occurs in many species before temperatures decline.

If woody plants are grown in the greenhouse on different photoperiods but with other environmental variables held constant or varied the same for all daylengths, their photoperiodic response is quickly apparent. A great many species stop growing almost immediately if subjected to daily photoperiods of 8, 10, or 12 hours even though the temperature is not limiting. Most of these same species grow for much longer periods, and some of them indefinitely, on photoperiods of 16 or more hours per day. Such results are obtained under conditions of essentially equal light energy regardless of differences in daily light duration. Differences in photosynthesis are thus excluded as the cause of the differences in response.

Effects of Short Photoperiods on Growth

When trees are subjected to photoperiods short enough to stop growth of their shoots, one of the first effects is a decrease in elongation of newly formed internodes

(Downs and Borthwick, 1956b; Downs, 1957). Simultaneously, the plant develops resting buds typical of its kind. In some species, such as *Liriodendron tulipifera* L. and *Betula mandshurica* (Regel) Nakai, this entails no important structural modification of the foliar primordia produced by the terminal meristem because no bud scales are formed. The stipules perform the function of scales and so the formation of a bud by such a plant results from almost complete stoppage of elongation of newly formed internodes, suppression of development of newly differentiated leaf primordia and probably a lowering of the rate of differentiation of new primordia.

In other species, such as *Liquidambar styraciflua* L., the buds are enveloped by bud scales. This means that one of the first evidences of bud formation is the production of scale primordia by the terminal meristem. When photoperiodic conditions are such that bud formation occurs, the meristem produces many bud scales and then resumes the production of primordia of normal foliaceous leaves. As in *Liriodendron*, the elongation of internodes is reduced to a minimum and the rate of production of new structures appears to slow down. In some of our daylength experiments a few *Liquidambar* trees initiated two or three bud scales in response to one of the daylength treatments, but then they resumed the production of typical foliage leaves without proceeding further with the formation of a bud. These sporadically formed bud scales remained attached at their respective nodes for a time and became separated from each other by internodes of appreciable length.

In still other species such as *Catalpa bignonioides* Walt. and *C. speciosa* Warder, cessation of growth in response to short days is accomplished by abscission of the terminal. One of the first observed effects, however, is again suppression of elongation of newly formed internodes. One of these internodes presently begins to blacken and soon it is abscised, carrying with it the entire stem apex. When growth is resumed, it occurs from axillary buds. Thus, growth of *Catalpa* is sympodial (fig. 1).

Growth on short days continues for many weeks in species such as *Ulmus americana* L. but eventually ceases. Other woody plants such as *Pyracantha coccinea* Roem. seem to grow as well on short days as on long ones. Certain woody plants from the Tropics are as responsive to daylength as many of those from the temperate zone. *Rauvolfia vomitoria* Afzel. and *Theobroma cacao* L., for example, grow more vigorously on 16-hour days than on 8- and 12-hour ones, a point of special interest because in the Tropics daily durations of light as great as 16 hours are never encountered in nature. On 8-hour photoperiods neither of the species stopped growing completely during the several month period of the test, but the rates were very low.

Although short-day treatments result in stoppage of terminal growth of shoots of a great many trees, they retain their leaves in most cases for many months. The leaves of such trees generally become chlorotic and may exhibit minor structural malformations similar to those of trees suffering from nutritional disturbance. Unbalanced nutrition may, in fact, be a secondary effect of short-day treatments. We have observed that the addition of fertilizer to *Cornus florida* L. in amounts fully acceptable on long-day treatments results in the quick death of the trees on short days.

Temperature operating directly or interacting with light is also effective in stopping length growth of trees, but our own experiments have not yet examined this possibility extensively. Such an effect could be one in which temperature changes the responsiveness of the plant to light, or temperature might operate through completely different pathways. It is sufficient, where the emphasis is on light and its mode of action rather than on final response, to point out that in woody, as in non-woody plants, a photoreaction controls growth. This photoreaction expresses itself through the photoperiodic mechanism, and is thereby

identified with the photoreaction controlling flowering. It also expresses itself through wide non-photoperiodic responses, which will be presented after further effects of photoperiod on tree growth are described.

Maintenance of Continuous Growth

Trees such as *Cornus florida* and *Acer rubrum* L. (Downs and Borthwick, 1956b) and shrubs such as *Weigela florida* var. variegata (Bean) Bailey (Downs and Borthwick, 1956a) can apparently be kept in a continuous state of shoot elongation

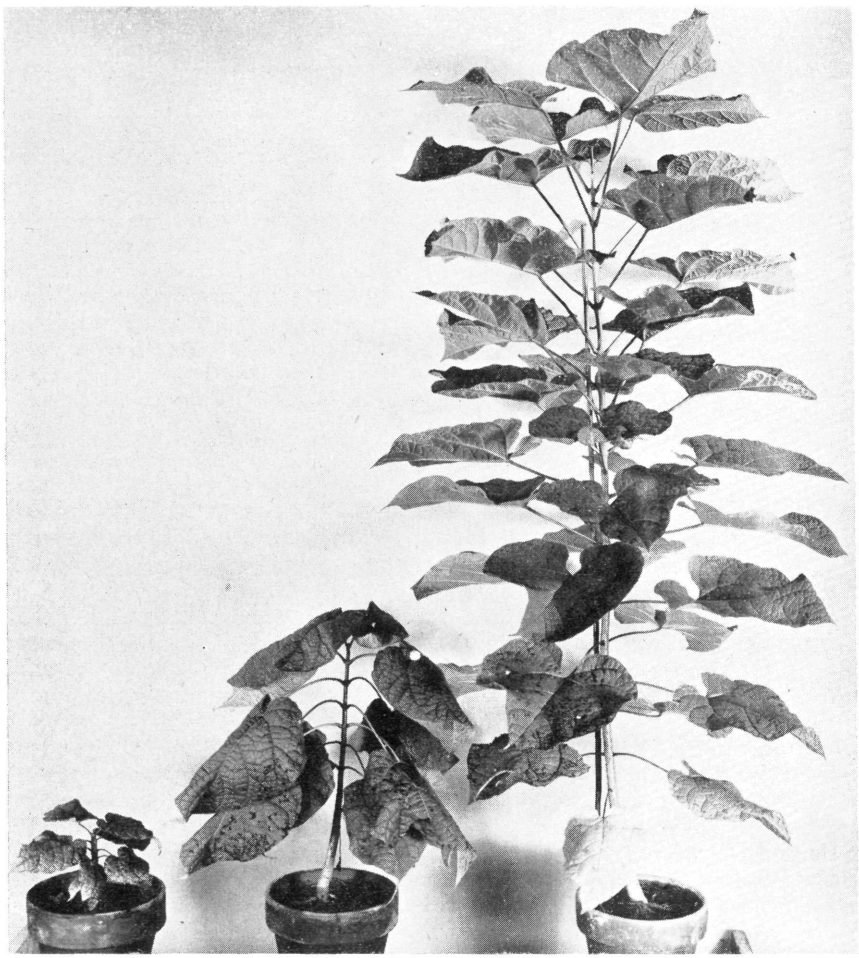

FIGURE 1. *Catalpa bignoniodes* grown on 8- and 16-hour photoperiods. Left: 23 weeks of 8-hour photoperiods. Center: 8 weeks of 16-hour followed by 15 weeks of 8-hour photoperiods. Right: 23 weeks of 16-hour photoperiods.

if they are constantly subjected to long-day treatment and the elongation can be stopped abruptly by short-day treatment. Other kinds of woody plants such as species of *Pinus* and *Quercus*, however, stop growth and form terminal buds even though long photoperiods are maintained continuously. After a period of inactivity the buds break, new flushes of leaves are produced and again buds are formed. This type of growth has been observed to persist in these genera for

several months under experimental conditions in the greenhouse. In nature the growth of these plants follows a similar pattern except that in some species a single flush and in others only two occur in a year. The inhibitory effect of the shortening summer days could obviously account for the lack of additional flushes of growth, but the possible inhibitory effects of other factors are not excluded.

The daily duration of light required to maintain growth of woody plants varies widely with the species. For several a sharp change in effect from inhibition to promotion of growth occurs when the daylength is increased from 12 or fewer hours to 14 or more hours per day. For others such as *Aesculus hippocastanum* L. no duration of light, including continuous, prevents early cessation of growth, but *Aesculus* makes appreciably more growth on long photoperiods than on short ones.

Conditions Including Resumption of Growth

Growth of a woody plant stopped by short photoperiods can sometimes be made to resume by subjecting the plant to long photoperiods. Examples are *Weigela* and *Cornus*. Others such as *Catalpa* and *Aesculus* require a few weeks of low temperature, whereas defoliation is adequate for trees such as *Paulownia*, especially if they are simultaneously given continuous light. *Weigela* will resume growth even on short days if defoliated, but as soon as the new shoots are formed their further growth is inhibited by the short photoperiods. While short-day treatment is thus an effective means of stopping growth of many trees, long-day treatment is not an assured means of either maintaining growth or inducing its resumption. Its effectiveness depends on the kind of plant and on conditions other than light.

Tree Growth as Influenced by Light Quality

Another aspect of light responsiveness of trees is illustrated by their reactions to light from incandescent-filament and fluorescent sources. Extension of a short day of natural light with either of these types of artificial light is effective in maintaining continued growth of plants such as *Catalpa*. The character of the growth, however, differs markedly, the trees receiving incandescent-filament light becoming appreciably taller than those receiving fluorescent light. In tests with *Catalpa* the average numbers of nodes produced during an experimental period of several weeks were the same, but the average internode lengths of plants receiving incandescent-filament light were twice those of ones receiving fluorescent light. This difference in effect results from differences in spectral composition of the two kinds of light and there is good evidence that the basic light reaction responsible for the difference is the same as that which makes photoperiodic control of growth of trees possible. Our knowledge of this reaction comes mainly from studies of such diverse phenomena as flowering (Borthwick *et al.*, 1952a), elongation of internodes (Hendricks *et al.*, 1956; Downs, 1955; Downs *et al.*, 1957), seed germination (Borthwick *et al.*, 1952b; Borthwick *et al.*, 1954; Toole *et al.*, 1955) and pigment formation (Piringer and Heinze, 1954; Mohr, 1957; Siegelman and Hendricks, 1957), and although not based immediately on work with trees, it is fully applicable to them.

The Photoreversible Reaction

The photoreaction responsible for so many apparently unrelated phenomena is caused mainly by red light, and the action of red is reversed by the so-called far-red wavelengths. The far-red or near-infrared region of the spectrum covers roughly the wavelength band of 7000 to 8000 Å. The wavelength regions of most effective action are about 5500 to 7000 Å for the red, with a maximum at about 6500 Å, and about 7000 to 7500 Å for the far-red reversal of the red effect, with a maximum near 7350 Å.

Specific effects of the red radiant energy are inhibition of flowering of short-day plants, promotion of flowering of long-day plants, promotion of seed germination prevention of stem elongation under certain circumstances, and promotion of the formation of certain plant pigments. Far-red radiant energy applied after red reverses these effects. Most of these phenomena are repeatedly reversible by

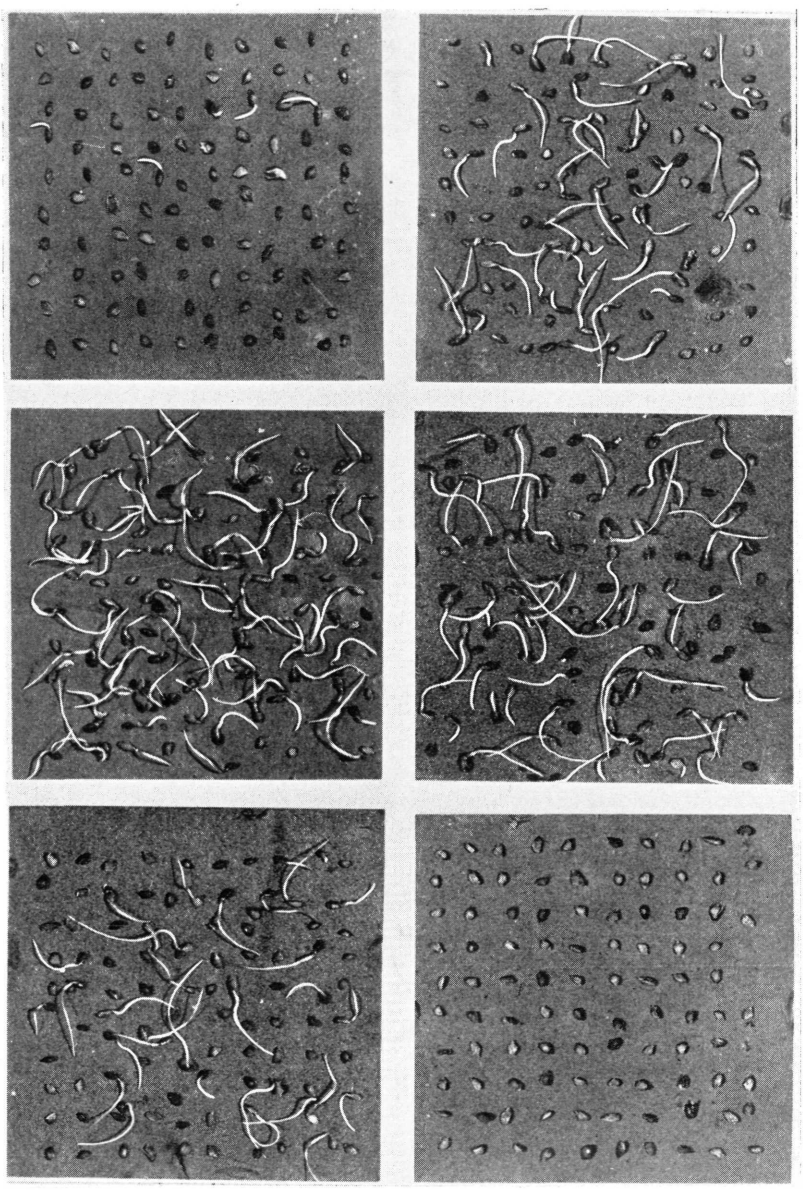

FIGURE 2. Effects of red and far-red radiant energy on the germination of seeds of *Pinus virginiana*. Treatments from left to right upper row—unirradiated control and 4 minutes of red: middle row—16 and 64 minutes of red; lower row—64 minutes red followed by 4 and 16 minutes, respectively, of far-red.

red and far-red and the ultimate response of the plant is determined by the kind of radiant energy used last in such a series of alternations.

Red and far-red radiant energies are obtained in very pure form by the use of a spectrograph of proper design (Parker *et al.*, 1946). They can also be had in sufficiently pure form for many kinds of experiments from ordinary lamps fitted with inexpensive filters. A suitable source of red radiant energy is a fluorescent lamp with a red cellophane filter, which removes most of the radiant energy of wavelength shorter than about 5500 Å. The fluorescent lamp is selected because it emits relatively little energy in the region from 7000 to 8000 Å. A satisfactory source of far-red energy is an ordinary incandescent-filament lamp. A filter consisting of two layers of blue and two of red cellophane effectively removes the visible light, leaving the far-red radiant energy in adequately pure form. With such sources and filters, one can perform typical reversibility experiments involving any of several kinds of responses.

The operation of this reversible photoreaction is illustrated by the control of internode length of young bean plants. The lengths attained by the second internodes of Pinto bean plants grown 8 hours per day under high-intensity fluorescent light depended on which of two kinds of radiant energy was given for a 5-minute period immediately after the fluorescent light was turned off. If the plants received far-red, the internodes became 3 to 3 and ½ times as long as those given red at the beginning of darkness. If the plants were subjected first to far-red and then to red, the promotive effect of far-red on elongation was nullified by the red and the internodes remained as short as those of unirradiated control plants placed directly in darkness at the close of the period of high-intensity fluorescent light. The photoreversible red-far-red reaction is thus regulatory of stem length of beans.

Effects of Mixtures of Red and Far-Red Radiant Energies

One might wonder what would happen if both kinds of light were given at the same time. This is actually what generally occurs because our usual light sources emit red and far-red simultaneously but in ratios characteristic of the source. Incandescent-filament light and sunlight are kinds that contain large amounts of both, and fluorescent light also is high in red but extremely low in far-red, though not devoid of it.

If bean plants are given 8 hours of high-intensity fluorescent light followed by a few hours of low-intensity light, their internodes elongate greatly if the low-intensity source is an unfiltered incandescent-filament lamp, and almost not at all if it is an unfiltered fluorescent lamp. In this instance the plants respond to the unfiltered incandescent light as if it were almost pure far-red radiant energy. The difference in degree of elongation of *Catalpa* internodes in unfiltered fluorescent and incandescent-filament light is clearly the result of the same reaction as that in the bean.

Although *Catalpa* and bean plants respond to the radiant energy from incandescent-filament lamps as though it were predominantly far-red, some plants react to it as if it were predominantly red. Thus, incandescent-filament light, like pure red light, given in the middle of a long dark period prevents flowering of short-day plants. These plants are so much more responsive to the red than to the far-red in the mixture that they react to this unfiltered light as if it were mainly red. If one now removes the visible radiant energy, particularly the red, by the use of filters that do not remove the far-red energy, the flowering stimulus is reestablished in the plants by continuing the treatment a few minutes more with the same lamps.

Seeds of pepper grass (*Lepidium virginicum* L.) exhibit an analogous response. They germinate readily if given a few minutes of unfiltered incandescent-filament light, but their germination is reinhibited if they are covered with blue cellophane

which removes the red but not the far-red energy. Seeds of henbit (*Lamium amplexicaule* L.), on the contrary, germinate in darkness and in unfiltered fluorescent light, but their germination is prevented by unfiltered incandescent-filament light. The mixture of red and far-red in incandescent-filament light thus acts as red on *Lepidium* seeds and as far-red on *Lamium*. Germination in both plants is controlled by the same reactions, but the final response depends on the relative sensitivity of each type of seed to the opposing actions of red and far-red radiant energy.

Light Responses of Tree Seeds

Many tree seeds are light-sensitive for germination. Seeds of *Ulmus americana* (Toole *et al.*, 1957), for example, are promoted by red and inhibited by far-red. The same is true of seeds of various species of *Pinus* (fig. 2). A single brief period of irradiation with red promotes germination of a very high percentage of the seeds of *Pinus virginiana* Mill. (Toole *et al.*, 1956a), provided the temperature is held within the rather narrow limits favorable to germination, but repeated treatments frequently induce higher germination of certain other species (Toole, 1957, personal communication). This suggests that the conditions favorable to germination established by a treatment with red light are transitory and must be reestablished at daily or more frequent intervals if germination is to proceed, but other explanations are possible. For some trees brief daily treatments with light are far less effective in promoting germination than treatments for several hours per day. Seeds of *Betula pubescens* Ehrh., for example, were found by Black and Wareing (1954) to germinate much better with long daily periods of irradiation than with short ones; so they concluded that in such a case germination was a photoperiodic response. This is probably correct, and it is important to keep in mind here, as in the photoperiodic control of flowering, that the period of time measured by the seed is probably the dark time and that the function of the long photoperiod is not to increase the total radiant energy but to reduce the duration of continuous darkness each day. This is illustrated by unpublished results of Downs (personal communication) and Toole (personal communication) with seeds of *Puya berteroniana* Mez and certain species of *Pinus* in which they found that a long photoperiod induced no higher percentage germination than did a few minutes of light given at both ends of an equally long period of darkness.

CONCLUSIONS

In a brief discussion of light effects on tree growth and seed germination such as this only the most obvious ones can be mentioned. These effects, although diverse in outward manifestation, are the result of a single basic photochemical reaction. This reaction occurs very widely, probably universally, in higher plants and is also known in lower ones such as ferns and possibly others. An outstanding characteristic of the reaction that makes its identification as the cause of widely different responses positive is its photoreversibility by red and far-red radiant energies. Further characteristics are that it is saturated in either direction by very low energies and that in darkness it goes slowly from the red-saturated to the red-requiring condition. Although the light-energy requirements are low, the effects on the plants are great. This could imply that a product formed by the red or far-red treatment has characteristics of an enzyme or other energy-transferring device that participates in reactions leading to a particular response.

Although knowledge concerning the light reaction has come principally from other plants, the reaction is known to occur in trees and to be responsible for many diverse responses in them. Further study of the light reactions of trees gives promise of information important not only to our understanding of its operation in plants in general but to various other aspects of tree physiology.

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DISCUSSION

DENNIS RICHARDSON (*University of Aberdeen, Scotland*): Is there any critical evidence that the Red-Far-Red reactions is involved in any of the known photoperiodic responses among animals as well as plants?

H. A. BORTHWICK: So far as I know there is no evidence that the photoperiodic responses of animals result from the Red-Far-Red reaction.

DENNIS RICHARDSON (in reply to a question concerning the possibility of light effects on the germination of pine having a so-called hard seed coat): Seed coats may be deceptive in their ability to transmit light. We have evidence in the case of Douglasfir that as much as 30 percent of the incident light may be transmitted by the seed coat and, when the coat is water saturated, as much as 50 percent. In view of the low light requirements of this type of response, the fact that so-called hard seed coat species respond to light cannot in my view be taken as evidence that the site of the light stimulus is in the seed coat itself. Other evidence suggests, in fact, that this is not so.

L. S. MINCKLER (*U. S. Forest Service, Carbondale, Illinois*): At what stage of germination is exposure to light effective? Apparently many spectus do not require such light exposure. Is that correct?

H. A. BORTHWICK: Seeds in the dry state are not significantly affected by light, but they often become responsive to light as soon as they start to imbibe water. It is true that many seeds are able to germinate in the dark. This does not necessarily mean that the light reaction does not occur in them, but it indicates that other pathways leading to germination are also present.